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Effects of changing seawater temperature on photosynthesis and calcification in the scleractinian coral *Galaxea fascicularis*, measured with O_2, Ca^{2+} and pH microsensors*

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SUMMARY: Single polyps of *Galaxea fascicularis* were fixed to glass vials with underwater epoxy resin. After regeneration into microcolonies they were used for microsensor measurements of photosynthesis and calcification under different incubating temperatures. Gross photosynthesis was found highest at temperatures of 23 and 26ºC (ca. 0.022 mole O_2 m^{-3} s^{-1}), close to the ambient temperature (i.e. 26ºC). At 35°C, gross photosynthesis was irreversibly inhibited as the microcolonies bleached. The net photosynthesis rapidly decreased with temperature and became negative at temperatures higher than 29ºC. Profiles of O_2 and Ca^{2+} showed a strong effect of temperature on them. The concentrations of Ca^{2+} measured on the polyp surface also showed temperature dependence of Ca^{2+} uptake. In the dark and below 29ºC, the surface Ca^{2+} concentration was temperature independent. During illumination, the surface Ca^{2+} concentration showed a dip at 26 ºC (ca. 8.7 mM), indicating maximum uptake rates at ambient temperature. However, at 32ºC and higher, Ca^{2+} was slightly higher at the tissue surface than in the seawater, in both light and dark, resulting from calcium dissolution. The surface pH in light increased gradually from 8.3 to 8.6 with increasing temperature to 23ºC, and thereafter remained constant to 29ºC. At 32 ºC, the pH became slightly acidic compared with the water phase, probably due to a decrease in the uptake of CO_2 by photosynthesis. The largest difference in pH between light and dark incubations was at temperatures between 23 and 29ºC (7.5-7.7 in dark versus 8.6-8.7 in light), which indicate high rates of photosynthesis and respiration in this temperature range . It is concluded that photosynthetic activity in the coral is maintained up to rather high temperatures (32ºC), but corals at super-optimum temperatures (above 26ºC) consume more O_2 than they produce, decalcify and produce CO_2.

Keywords: temperature, coral, gross photosynthesis, net photosynthesis, calcification, *Galaxea fascicularis*, microsensors..

RESUMEN: EFECTOS DEL CAMBIO EN LA TEMPERATURA DEL AGUA EN LA FOTOSÍNTESIS Y LA CALCIFICACIÓN DEL CORAL ESCLERACTINIARIO *GALAXEA FASCICULARIS* MEDIDOS CON MICROSENSORES DE O_2, Ca^{2+} Y pH. – Se fijaron pólipos de *Galaxea fascicularis* sobre viales de cristal con resina epoxy. Una vez generaron pequeñas colonias se utilizaron como sensores para medir los cambios en la fotosíntesis y calsificación a diferentes temperaturas. Los valores de fotosíntesis total (bruta) fueron más elevados a temperaturas entre 23 y 26°C (ca. 0,022 mole O_2 m^{-3} s^{-1}), similares a los del ambiente (26°C). A valores de 35°C, la fotosíntesis total se inhibió irreversiblemente y las pequeñas colonias se blanquearon. La fotosíntesis neta disminuyó rápidamente con la temperatura hasta llegar a valores negativos en temperaturas mayores de 29°C. Los perfiles de O_2 y Ca^{2+} mostraron un elevado efecto de la temperatura. Las concentraciones de Ca^{2+} medidas en la superficie de los pólipos también mostraron una influencia en la incorporación de Ca^{2+}. En condiciones de oscuridad y temperatura por debajo de 29°C, la concentración de Ca^{2+} era dependiente de la temperatura. En periodos iluminados, el Ca^{2+} concentración mostró un pico 26°C (ca. 8,7 mM) hecho que indicaba una tasa de incorporación a temperatura ambiente. hecho que indica que las máximas incorporaciones se efectuaron a temperatura ambiente. Sin embargo, a 32°C o más, los valores de Ca^{2+} fueren ligeramente altos en la superficie del tejido que en agua de mar, en ambas situaciones de iluminación y oscuridad, resultado de la disolución de la disolución de Calcio. El pH en periodos iluminados se incrementó ligeramente de 8.3 a 8.6, incrementándose la temperatura se y permaneció constante hasta 23°C aunque permenecía constante hasta los 29°C. A 23°C el pH se transformó en un pH ligeramente ácido, probablemente debido a la disminución de en la tasa de retención de CO_2 mediante la fotosíntesis. Las mayores diferencias en pH en peiodos iluminados y oscuros fue de 23-29°C (7.5-7.7 en oscuridad versus 8.6-8.7)

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lo que infica un alta tasa de fotosíntesis y respiración a estos datos en este margen de temperaturas. La conclusión del trabajo es que, la actividad fotosintética en el coral es claramente elevada y se mantiene alta a temperaturas hasta alcanzar los 32°C, pero los corales, en el periodo óptimo de temperaturas de verano (por encima de 26°C) consume mas O_2 que el que produce, se descalcifica y produce CO_2.

Palabras clave: temperatura, coral, fotosíntesis total, fotosíntesis neta, calcificación, *Galaxea fascicularis*, microsensores.

INTRODUCTION

Coral reefs are tropical shallow water ecosystems largely restricted to the seas between the latitudes of 30° north and 30° south of the equator, where temperature ranges between 18 and 30 ºC (Spalding *et al.,* 2001). Scleractinian corals are the main constituent of the coral reefs. These are benthic animals that form colonies of varying shapes, colours and sizes. The building block of each colony is called a polyp. The body of the coral is formed mainly from an exoskeleton of $CaCO_3$ deposited by the animal and a thin layer of living tissue covering the skeleton. The corals feed on zooplanktons and other suspended organic matter from the surrounding seawater (i.e. heterotrophy) (Porter, 1976). In addition to this, the animals live in a symbiotic relationship with plant-like dinoflagellates called *Symbiodinium* sp., commonly known as zooxanthellae, which photosynthesize using light energy to produce oxygen and organic matter for the benefit of the animal (i.e. autotrophy). This symbiotic relationship is crucial for the survival of the coral in an environment described as a desert in terms of nutrient content (Sorokin, 1995; Hoegh-Guldberg, 1999).

Coral reefs are threatened by many anthropogenic and environmental factors, some of which are the increased atmospheric CO_2 and the associated decrease in aragonite and calcite saturation states, increased sea surface temperature, coral diseases, eutrophication and pollution (Smith and Buddemeier, 1992; Brown, 1997; Hodgson, 1999; Leclercq *et al.,* 2000; Kleypas *et al.,* 2001). In their weakened conditions, coral reefs will be less able to cope with rising sea levels and other anthropogenic stresses, which are expected in the middle of this century (Langdon *et al.,* 2000). By the end of the century, global warming is expected to kill most of the presently existing coral reefs (Pockley, 1999).

One of the consequences of the increased sea surface temperature is coral bleaching, by which the coral turns pale or white in colour as a result of losing its symbiont and/or the pigmentation. Coral bleaching events have increased in frequency and severity, due mainly to high water temperatures associated with El Niño–related warming and a general warming trend. This temperature effect on corals was first recognised after the 1982-1983 El Niño/Southern Oscillation (ENSO) event through which massive coral bleaching occurred after being exposed to unusually high water temperature (Glynn, 1988). Since that event, coral bleaching has occurred on a regular basis in many places of the world (reviewed by Brown, 1997). From mid-1997 to late 1998, catastrophic bleaching with massive coral mortality has been reported from many areas of the world (e.g. Wilkinson and Hodgson, 1999; Lough, 2000; Vargas-Angel *et al.,* 2001; Jimenez *et al.,* 2001; Carriquiry *et al.,* 2001; Bruno *et al.,* 2001; Podesta and Glynn, 2001). The amount of bleaching and mortality was similar to that reported in the 1982-1983 bleaching event (Glynn *et al.,* 2001).

While many studies on the effects of temperature on corals have focused on coral bleaching and its mechanism, little is known about the effects of temperature on the metabolic processes in coral. The main biogeogenic processes of corals are photosynthesis (O_2 production, CO_2 binding), respiration (CO_2 release) and calcification (Ca^{2+} uptake, CO_2 release), and obviously the balance between these is crucial for the net exchange of corals and seawater. It is thought that calcification can balance the pH effect of photosynthesis, and thereby alleviate the CO_2 limitation for photosynthetic activity (McConnaughey, 1994). The effect of temperature on the metabolic rates was studied through the use of entire colonies with inherent variation in phenotype and genotype. A better comparison of experiments became possible through the use of micro-colonies originating from the same parent colony (Al-Moghrabi *et al.,* 1993). The new application of microsensors permitted the measurement of many parameters at a μm scale and with high spatial and temporal resolution (De Beer *et al.,* 2000; Kühl *et al.,* 1995; Al-Horani *et al.,* 2003a; Al-Horani *et al.,* 2003b; Al-Horani *et al.,* 2005). In this study, the two advancements were combined to investigate the impact of temperature on the physiology of the scleractinian coral *Galaxea fascicularis*.

MATERIALS AND METHODS

Coral sample

Galaxea fascicularis colonies (6 parent colonies) were collected by SCUBA diving from about 5 m depth from the Gulf of Aqaba (Jordan) south of the Marine Science Station. The collected colonies were wrapped in plastic bags and transported to the Max Planck institute in Bremen-Germany, where they were kept in a 540 l artificial seawater tank (35 salinity, 26ºC, 140-μmole photons m^{-2} s^{-1} with a light spectrum and intensity similar to natural light, 12 h/12 h light-dark cycle). Single polyps of *G. fascicularis* were fixed to glass vials with underwater epoxy resin. After about 4 weeks the polyps regenerated into microcolonies and were used for microsensor measurements.

Microsensors

Ca^{2+} microsensors (de Beer *et al.,* 2000), Clark type O_2 electrodes (Revsbech and Jorgensen, 1983) and liquid ion exchange (LIX) pH electrodes (De Beer *et al.,* 1997) were constructed and calibrated as described. In addition to the external calibration described in the literature, calcium and pH electrodes were internally calibrated by correcting the values measured by the electrode with the actual values of the seawater since shifting of the electrode reading can happen in seawater environment. The electrodes were positioned on the surface of *G. fascicularis* with the help of a micromanipulator and observation with a dissecting microscope as described in (Kühl *et al.,* 1995). The surface position was considered as zero level in terms of depth. Profiles of O_2 and Ca^{2+} were done by stepwise moving of the electrodes away from the surface and recording the reading at each depth. The slopes which originate from the plots between the depth and the values measured for O_2 and Ca^{2+} were used to calculate the fluxes of O_2 (i.e. net photosynthesis) and Ca^{2+} using Fick's first low of diffusion, assuming zero diffusion into the skeleton. Gross photosynthesis (i.e. total oxygen production) was measured by the light-dark shift method according to Kühl *et al.,* (1995). The respiration (R) in light was calculated from the difference between gross (Pg) and net (Pn) photosynthesis according to the equation:

$$Pg = Pn + R.$$

Experimental set-up

Coral colonies were placed in a polycarbonate flow cell for microsensor measurements. Filtered seawater was circulated between the flow cell and a 10 l reservoir at a constant flow rate (420 ml/min). The reservoir was continuously aerated. A motorised micromanipulator fixed on a heavy stand was used to position the electrodes on the polyp tissue surrounding the mouth opening. A halogen light source (KL 1500, Schott Mainz company, Germany) provided a light intensity of 140-μmole photons m^{-2} s^{-1}. A shutter (Unibliz Electronic) controlled the entrance of light. Signals from the millivoltmeter and the picoamperometer were plotted on a strip-chart recorder.

RESULTS

The oxygen profiles on the surface of the *G. fascicularis* polyp showed that the surface level of oxygen is higher than its level in the incubating seawater at temperatures of 17-26°C which demonstrate export of oxygen to the seawater from the coral (Fig. 1). At 29°C, the level of oxygen started to decrease compared with the ambient level, although the level remained higher than the seawater oxygen level. At 32°C and 35°C, the O_2 level became negative compared with the seawater level, showing an influx of oxygen from the seawater rather than efflux.

Gross photosynthesis (Pg) (i.e. total O_2 production) increased with increasing temperature from 17°C (0.009 mole O_2 m^{-3} s^{-1} ± 0.001) and reached its highest rate at 23 and 26°C (ca. 0.022 mole O_2 m^{-3} s^{-1} for both temperatures) (Fig. 2). The rate started to

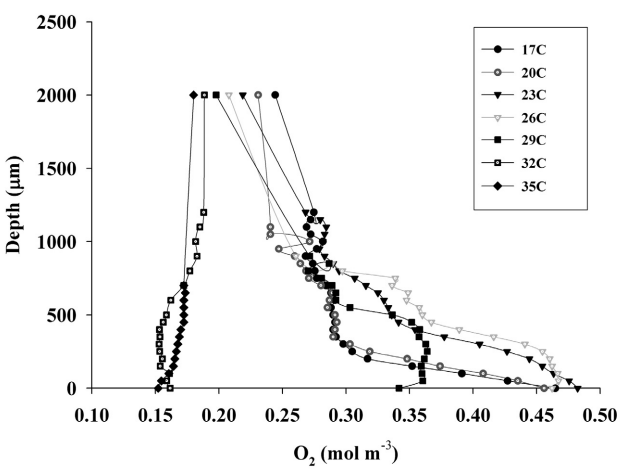

FIG. 1. – Oxygen profiles on the surface of *G. fascicularis* at different temperatures.

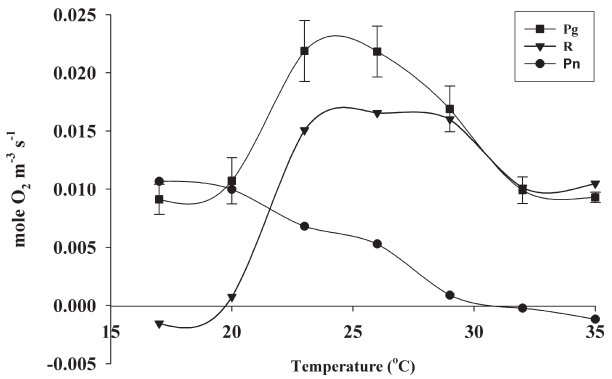

FIG . 2. – Gross and net photosynthesis and respiration rates at different temperatures. Pg: gross photosynthesis, Pn: net photosynthesis, R: light respiration.

decrease after that, reaching its lowest at 35°C (0.009 mole O_2 m^{-3} s^{-1} ± 0.0004), at which the coral bleached. Unlike Pg, the net photosynthesis (Pn) rate was highest at low temperatures and started to decrease with increasing temperature. The Pn was close to zero at 29°C (0.0009 mole O_2 m^{-3} s^{-1}) and became negative (i.e. influx of O_2) at temperatures higher than 32°C (Fig. 2).

The pH measured at the coral surface was also influenced by the changes in temperature (Fig. 3). In light, the pH increased from 8.3 to 8.6 with increasing temperature to 23°C, after which the surface pH remained constant at around 8.6. At 32ºC, the surface pH dropped to a level similar to the pH level of the incubating seawater (ca. 8.3). In dark, the surface pH was lower than the pH of the incubating seawater at all incubating temperatures. At temperatures below 20ºC, the pH was higher than 8 and decreased with increasing temperature to reach about 7.5 at 32°C (Fig. 3).

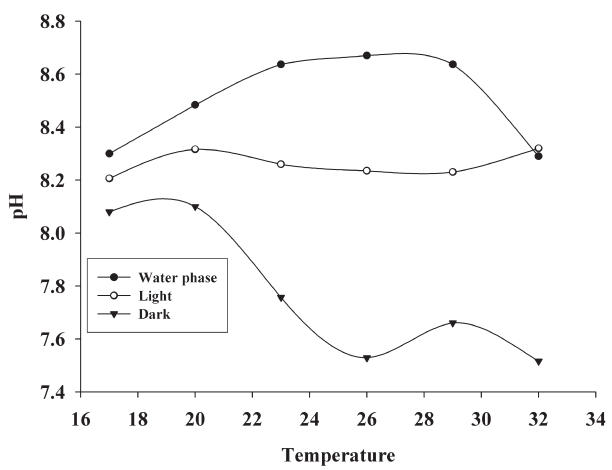

FIG . 3. – pH levels in light and dark on the coral surface at different temperatures.

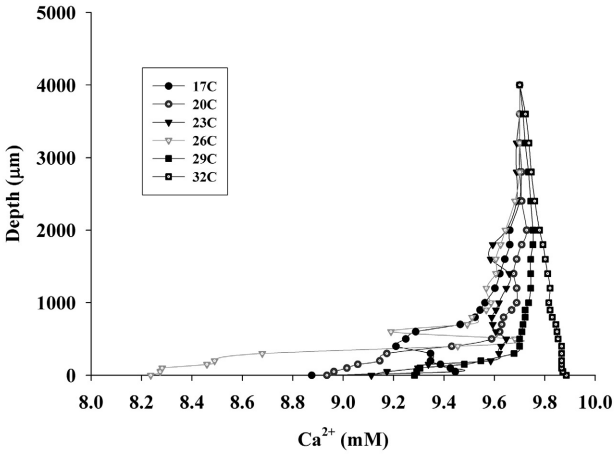

FIG . 4. – Calcium profiles on the surface of *G. fascicularis* at different temperatures.

The Ca^{2+} profiles on the polyp surface showed a strong effect of temperature, and the slopes at temperatures below 32°C indicate Ca^{2+} uptake from seawater and a slight release of Ca^{2+} to the seawater from the coral at 32°C (Fig. 4). The calculated Ca^{2+} fluxes (Fig. 5) showed that the influx of Ca^{2+} into the coral increases with increasing temperature, the optimum being around 26°C (0.146 μmole m^{-2} s^{-1}). After that, Ca^{2+} influx decreased with further increases in temperature, and at 32ºC a slightly negative flux (-0.005 μmole m^{-2} s^{-1}) was obtained (i.e. Ca^{2+} efflux was observed). The levels of Ca^{2+} at the coral surface in light and dark are shown in Figure 6. The data obtained showed that the coral maintain the level of Ca^{2+} on the surface below that of seawater in both light and dark conditions. In light, the level of Ca^{2+} was always below that of the dark condition at all incubating temperatures, except for that at 32°C, where the Ca^{2+} level became similar in both cases and close to that of the incubating seawater (i.e. 9.8 mM). In light, the lowest Ca^{2+} concentration

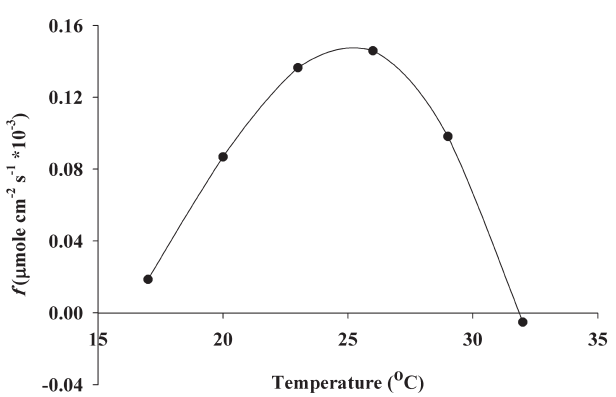

FIG . 5. – Calculated calcium fluxes at the surface of *G. fascicularis* at different temperatures. *f*; flux.

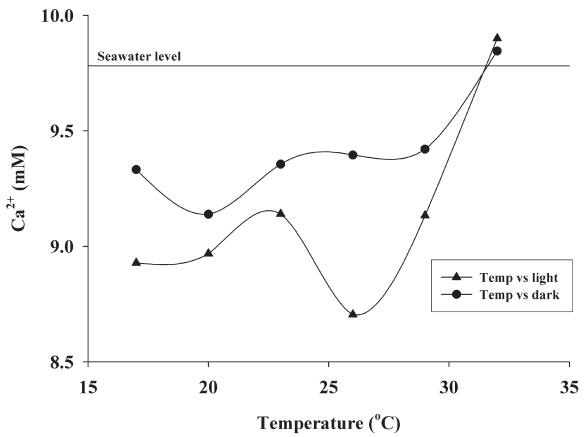

FIG . 6. – Calcium levels in light and dark measured on the surface of *G. fascicularis* at different temperatures.

on the surface was observed after incubating the coral at 26°C (i.e. close to the culture condition) and was equal to 8.7 mM (Fig. 6).

DISCUSSION AND CONCLUSION

The temperature effects on corals were first recognised after a massive coral bleaching was observed in many areas of the world following an unusually high sea surface temperature (Glynn, 1988). When coral bleaches, the zooxanthellae and/or the pigmentation are lost, making it look pale or white in colour, and eventually the coral dies. It has been shown that coral undergoes vast physiological changes before bleaching occurs, suffering oxidative stress as the activity of antioxidant enzymes increases (Lesser, 1997). Details of the effect of temperature on the physiology of corals (i.e. photosynthesis, calcification and respiration) are not well known; therefore this study addressed this question. At the beginning, profiles of oxygen on the coral surface were measured with increasing temperature. Such O_2 profiles reflect the O_2 fluxes between the coral and the incubating seawater. When the coral produces more O_2 than it needs, the extra O_2 is exported to the surrounding seawater (i.e. an efflux of O_2 is observed) and when the coral consumes more O_2 than produces, the O_2 deficit is compensated for by importing it from the surrounding seawater (i.e. an influx of O_2 is observed). At low temperature, the O_2 profiles on the polyp surface showed that the coral was producing more O_2 than it needed (Fig. 1). With increasing temperature, the difference between rates of O_2 production and consumption decreased, and at temperatures higher than 32 ºC the difference became negative (i.e. the coral started to consume more O_2 than it produced) so O_2 influx was observed (Fig. 1). The calculated net photosynthesis (Pn) revealed the same situation: at low temperatures Pn was highest (Fig. 2). The data obtained showed that Pn was highest at 17°C and decreased with increasing temperature to reach its lowest at 35°C, at which it was negative (i.e. the coral was importing O_2) (Fig. 2). On the other hand, gross photosynthesis (Pg), the total O_2 produced by the coral, behaved differently (Fig. 2). Pg was low at low temperatures (17-20°C) and increased with increasing temperature until a peak rate was obtained at temperatures between 23 and 26°C, after which Pg decreased with increasing temperature to reach its lowest at 35°C. This Pg behaviour is expected, since the coral started to bleach as inferred from its pale colour observed upon incubation of the coral at 35°C. Therefore with a decreasing number of zooxanthellae, the rate of O_2 production decreased, which was reflected by the low Pg rate measured at high temperatures. The role of temperature in coral bleaching was described as a photoinhibition process in which the heat stress leads to production of active O_2 by the light energy in the symbionts and the host tissues, which subsequently causes cellular damage and expulsion of symbionts (Lesser, 1997; Jones *et al.,* 1998; Hugh-Guldberg, 1999). This loss of zooxanthellae at high temperatures was suggested to be a final strategy to defend corals from oxidative stress (Downs *et al.,* 2002).

The O_2 budget in the coral is subject to a number of processes which produce and/or consume it. In light, O_2 is produced by the symbiont's photosynthesis. At the same time, O_2 is consumed in oxidative phosphorylation by which ATP is produced in the mitochondria of the coral and the symbiont. The O_2 is also consumed in photorespiration where Ribulose bisphosphate carboxylase oxygenase (Rubisco) uses O_2 to oxidize ribulose bisphosphate to phosphoglycolate and the Mehler reaction in which O_2 is reduced to superoxide by the reduced donors associated with photosystem I (Marx, 1973; Walker, 1992; Badger *et al.,* 2000). Photorespiration is not significant in zooxanthellae when they are present in the coral and the Mehler reaction is not significant in C-3 carbon fixation pathways such as the one characterising the zooxanthellae (Taylor and Trench, 1986; Streamer *et al.,* 1993; Badger *et al.,* 2000). Therefore, oxidative phosphorylation by the host and the symbiont is the only significant process consuming O_2 in light. The resulting ATP of this

process is used to power the biological activities in the coral. The amount of ATP needed by the coral is proportional to the coral activities. At low temperatures, the coral is not very active, so the amount of O_2 produced by photosynthesis is more than that needed by the coral and the excess O_2 is released to the seawater. When the temperature increases, the coral becomes more active and more ATP production is needed. Consequently, both O_2 production (Pg) and consumption (respiration) rates increase with increasing temperature, so the Pn rate, which represents Pg minus respiration, was high at low temperatures and low at high temperatures.

Like the O_2 budget, the surface pH is a function of a number of processes occurring in the coral host and the symbiont. Photosynthesis by the zooxanthellae fixes CO_2 and increases the surface pH. On the other hand, respiration by the coral and the zooxanthellae releases CO_2 and thereby decreases the surface pH. Protons produced during calcification (Al-Horani *et al.,* 2003a) can be used in CO_2 production through the action of carbonic anhydrase and may also influence the pH at the coral surface. Furthermore, H^+-ATPase, which pumps protons to the surface of the oral ectoderm (Furla *et al.,* 2000), also affects surface pH. The surface pH was higher in light than in dark conditions. This is because processes occurring in light favour a pH increase, while those occurring in dark tend to decrease pH. The prevailing processes in light, which influence the surface pH, are photosynthesis by the symbiont and respiration by the host and the symbiont. Although, the rate of light respiration is much higher than that of dark respiration (Al-Horani *et al.,* 2003a), the pH was higher in light than in dark. This is because the photosynthetic CO_2 fixation rate exceeds the rate of CO_2 release in light respiration (Al-Horani *et al.,* 2003b). In addition, much of the CO_2 released by respiration is fixed by photosynthesis and thereby the pH is maintained higher in light than in dark (Al-Horani *et al.,* 2003b). This high pH in light is important for the coral to calcify and build its calcium carbonate skeleton, since the coral do not calcify at low pH. In dark, photosynthesis stops completely and only respiration is maintained. The pH did not go too low because the rate of dark respiration is low. This is due to the fact that corals are less active in light than in dark, as indicated by the lower rates of respiration and calcification in dark compared with light (Al-Horani *et al.,* 2003a, b), and therefore the need for ATP generation by respiration is greatly reduced in the dark. At high temperature, the pH decreased in both light and dark conditions indicating a higher rate of CO_2 release compared with its fixation rate by photosynthesis. This result is important in terms of the CO_2 budget of the sea in summer and or during the El Niño episodes. According to the results obtained in this study, the coral reefs are expected to start exporting CO_2 to the atmosphere rather than fixing it under such conditions, thereby exaggerating the well-known greenhouse effect. This observation needs further studies, though a similar observation was made at the community level (Kawahata *et al.,* 1997, 1999).

In light, Ca^{2+} uptake rates on the polyp surface were temperature-dependent, as was shown from the calculated fluxes (Fig. 5). The rate of uptake increased with increasing temperature to 26°C and no further increase was obtained at temperatures above this threshold. This result is similar to those obtained by Lough and Barnes (2000) in the coral *Porites lutea,* in which the average calcification rate increased with increasing sea surface temperature in the range 23-29°C. The temperature effect on calcification was not linear, since the rate started to decrease at temperatures above 26 ºC, as was also shown by the buoyant weighing technique at high temperatures in the coral *Stylophora pistillata* and the hydrocoral *Millepora dichotoma*. (Abramovitch-Gottlib *et al.,* 2002). The rate increase below 26°C is due to the fact that the calcification process in corals is enzyme-controlled (Ip *et al.,* 1991; Al-Horani *et al.,* 2003a). At 29°C, the coral started to bleach and lose its symbionts. Since coral calcification is an energy requiring process (Chalker and Taylor, 1975; Fang *et al.,* 1989), the loss of these symbionts, which together with heterotrophy supply the energy needed for coral calcification (Pearse and Muscatine, 1971; Porter, 1976; Muscatine, 1990; Buddemeier, 1994; Sebens *et al.,* 1996; Anthony, 2000), could be one reason for the observed decrease in Ca^{2+} uptake at high temperatures. In addition to this, the enzymes' activities, which control calcification, also decrease at high temperatures. Furthermore, the decreased photosynthetic CO_2 fixation at high temperature leads to a decrease in pH, thereby decreasing calcification in the coral.

Light clearly increased the concentration difference between seawater and tissue surface compared with the dark condition at moderate temperatures (Fig. 6). This suggests an enhanced calcification rate in light, as has been previously recorded (e.g. Goreau, 1963; Chalker and Taylor, 1975; Barnes and Chalker, 1990; Gattuso *et al.,* 1999). During illumination, the concentration of Ca^{2+} on the surface

showed a dip at 26°C (>10% below seawater calcium level), suggesting a maximum uptake rate at ambient temperature. At 32°C, the level of Ca^{2+} was high at the tissue surface relative to the seawater, in both light and dark conditions, suggesting Ca^{2+} dissolution. This could be due to the fact that the flux out of Ca^{2+} exceeds the influx at the coral surface, which might have resulted from the low pH and the decreased photosynthesis and enzyme activities at high temperature. In the dark and below 29°C, the surface Ca^{2+} concentration was temperature-independent. It was 2-5% below the seawater concentration due to dark calcification.

In conclusion, photosynthetic activity is maintained up to fairly high temperatures (32°C), but corals at super-optimum temperatures (above 29°C) consume more O_2 than they produce, decalcify and produce CO_2. The results obtained showed a direct link between calcification and photosynthesis in coral under stress conditions. This could further help to understand the coupling mechanism between the two processes in corals.

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